Notes on the Life Cycle and Natural History of Butterflies of El Salvador. II B.—*Hamadryas guatemalena* Bates (Nymphalidae-Hamadryadinae)

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Abstract: Observations on the adults and early stages of *Hamadryas guatemalena* Bates have been carried out in the vicinity of San Salvador, El Salvador, for a period of 4 years. In this article the results are presented for the first time, with a detailed account of the life cycle, illustrated with photographs, of the larval behavior and the plant used as food.

The characteristics of the species are compared with the characteristics of other closely related species. The contention that there should be several genera within the group is discussed.

As in other Nymphalidae, in this species the gaudy coloration and daring behavior of the larvae, and the use of a foodplant belonging to the Euphorbiacae (*Dalechampia scandens* L.) reputedly poisonous, suggest impalatability of the adults.

This is the second article of a series dealing with butterflies belonging to the genus *Hamadryas*, found in El Salvador. In this article we give an account of our observations on the early stages and adults of *Hamadryas guatemalena* Bates carried on since August 1970 in various zones of the country, mostly within 15 km from the capital city San Salvador. The first time we found larvae of this species was shortly after we started studies on a close relative, *H. februa* Hübner, during August 1970. As both species feed on the same plant, we ended up studying the two species simultaneously, which caused at first some confusion, as eggs collected produced at times two different kinds of larvae. The problem was solved when a female of *Hamadryas guatemalena* was observed ovipositing also on the same plant as *H. februa*. It is practically impossible to tell apart the eggs of one species from the other. As usual, eggs were collected just after oviposition and put in transparent plastic bags fastened with rubber bands. Emerged larvae were fed on fresh leaves of the foodplant replaced every three days until pupation. The bags were cleaned every day of excrement and excess humidity. The pupae were transferred to a wooden cage with mosquito-net covering, where the adults emerged. Bags and cage were kept indoors at all times under ambient light and temperature

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conditions. Notes were kept of the measurements and the duration of each phase of the metamorphosis. Specimens in alcohol were sent to the American Museum of Natural History, New York, where the adults were determined.

LIFE CYCLE STAGES

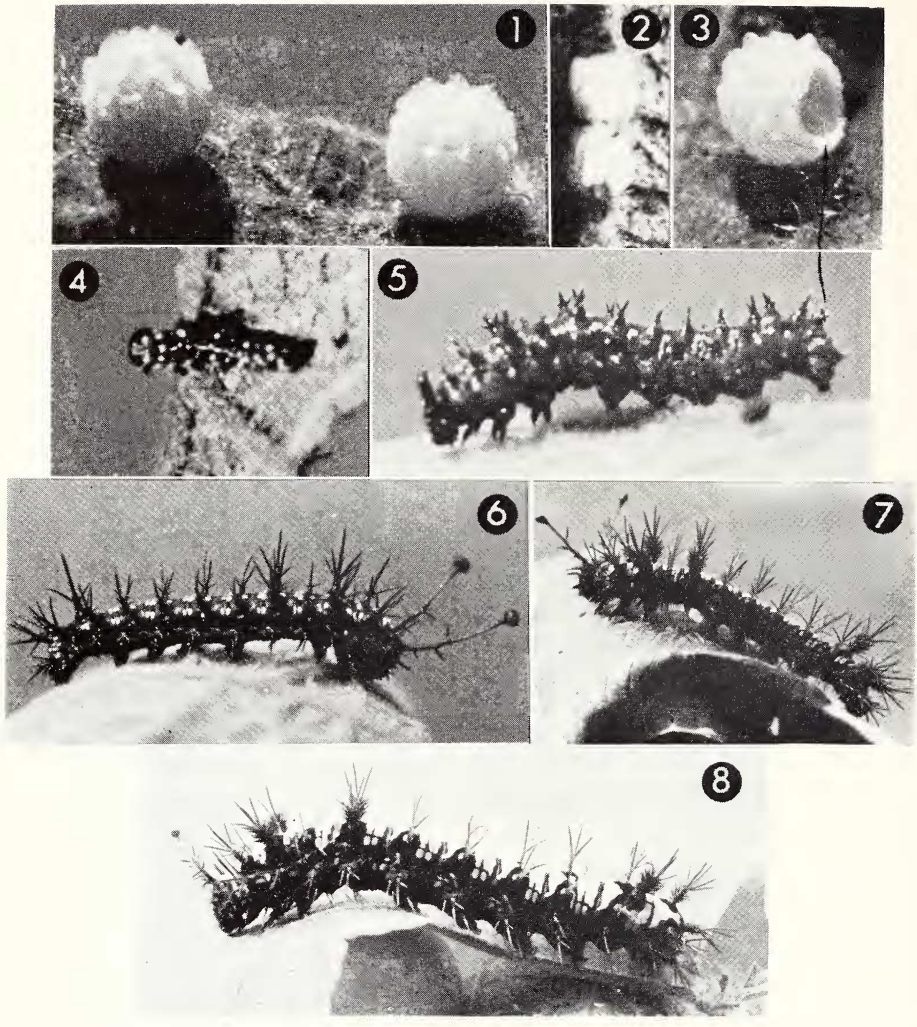
Egg. Pure white, almost round with small flat base and sculpturings starting basally with thick ribs which disappear about a third from the base and are substituted by irregular, rounded or sharp protuberances covering part of the wall and the micropylar area. About 1 mm diameter. Hatches in 3–5 days.

First instar larva. Head shiny black, slightly cordiform, naked. Body cylindrical, greenish-brown with lighter tubercules and sparse short setae. Legs and prolegs dark brown. About 3 mm when recently hatched, about 4 mm before moulting in 3 days.

Second instar larva. Head black with small white spines on lateral margins and frontal area. Short thick horns on apices of epicrania. Body dark brown with longitudinal rows of furcate short spines and four rows of white dots, two subdorsally and two supraspiracularly. About 7 mm long before moulting in 4 days.

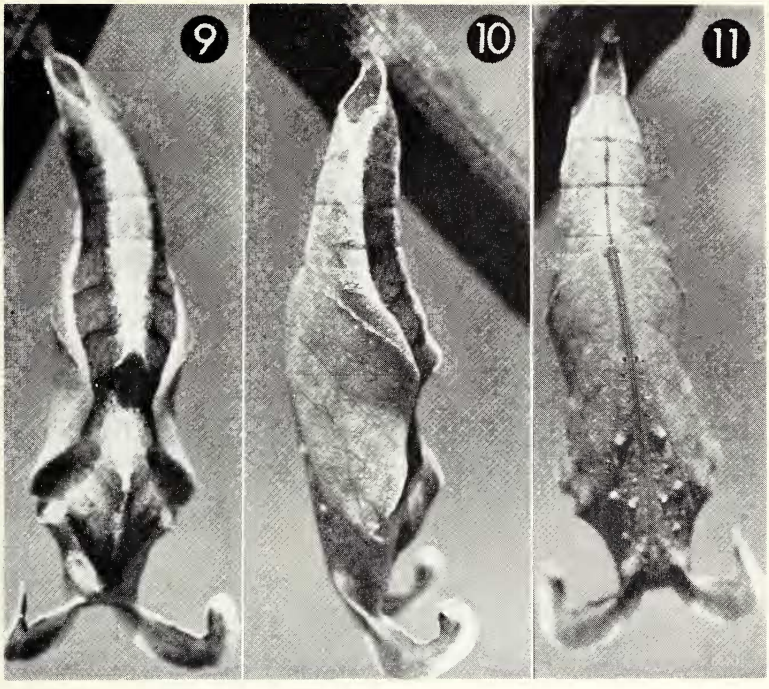
Third instar larva. Head black with long and slender horns on epicrania, two spines between their bases, three long spines on lateral margin of head and several short spines frontally; ocelli black, surrounded by sparse, short golden setae. The horns have basally on the shaft two accessory spines directed forward, a little higher two spines directed laterally and about the middle of the shaft two more spines directed inwards; the horns are tipped by a sphere armed with tiny spines. The body's ground color is black with longitudinal rows of yellow spots subdorsally and supraspiracularly. The spine arrangement is as follows: on first thoracic segment (T-1): one bifurcate subdorsal spine, one bifurcate supraspiracular spine and one simple subspiracular spine; on T-2: one prominent subdorsal 6-furcate spine, and 6-furcate supraspiracular spine, one small spiracular simple spine and one longer spine subspiracularly; on T-3: one most prominent 6-furcate subdorsal spine, one 5-furcate supraspiracular spine, one small, spiracular simple spine and two simple spines subspiracularly. On first abdominal segment (A-1): one 4-furcate subdorsal spine, one simple supraspiracular spine, one 4-furcate subspiracular spine and two supraventral simple spines. On A-2: one prominent 5-furcate subdorsal spine, one 3-furcate supraspiracular spine, one 4-furcate subspiracular spine sided by a simple spine, 3 supraventral simple spines. From A-3 to A-6: one 5-furcate subdorsal spine, one 3-furcate supraspiracular spine, one 4-furcate subspiracular spine sided by a simple spine and 2 simple spines supraventrally. On A-7 one very prominent dorsal 3-furcate spine, one 6-furcate subdorsal spine, one 3-furcate supraspiracular spine, one 5-furcate subspiracular spine sided by a simple spine and two simple supraventral spines. On A-8: one prominent 6-furcate dorsal spine, one prominent 6-furcate subdorsal spine, one 3-furcate supraspiracular spine, one 5-furcate subspiracular spine sided by a simple spine and two simple supraventral spines. On A-9: one 8-furcate subdorsal spine deflected caudad. On A-10: two simple spines, side by side, on anal plate. Grows to 1.3 cm in 4 days.

Fourth instar larva. Head as in third instar, with longer horns. Body ground color black with light yellow, very conspicuous dorsal oval patches forming an irregular and broken stripe from T-1 to A-9, and two supraspiracular light yellow dots on each abdominal segment. The shafts of the prominent subdorsal spines on T-2, T-3, A-2 and A-8, and of the median spines on A-7 and A-8 are armed by a host of small brown spinulets directed distally. Grows to 2.5 cm in 3–4 days.



FIGS. 1–8. *Hamadryas guatemalena* Bates. 1. Two eggs side by side. Notice the left is grayish, the other pure white. One hatched one day before the other. 2. Two eggs one on top of the other. Both hatched the same day. 3. Eggshell showing the exit hole on the side. 4. First instar larva. Notice frass pellets stuck on the body. 5. Second instar larva. 6. Third instar larva. 7. Fourth instar larva. Notice spinulets on some spines. 8. Fifth instar larva.

Fifth instar larva. The only change is that the body markings become bright deep yellow, and the horns on the head and spines on the body are dull yellow. Prominent subdorsal spines on T-2, T-3, A-2 and A-8 and dorsal spines on A-7 and A-8 look "hairy" due to the profusion of dark accessory spines on the shaft of the scoli. Grows to 4.2 cm in 4–5 days.



Figs. 9–11. *Hamadryas guatemalena* Bates. 9. Pupa, dorsal view. 10. Pupa, side view. 11. Pupa, ventral view.

Prepupa. Does not change in aspect, but for slight shortening of the body. Hangs from anal prolegs, with thorax incurved ventrally, for one day.

Pupa. Hangs rigidly anchored from flat cremaster. Abdomen thickens abruptly from cremaster and then gradually to base of wings, then narrows laterally and dorsally, forming a slight indentation, thickening again on thoracic segments, then narrows abruptly to head, which terminates in two flat prolongations diverging laterally from each other and incurved dorsally. The edges of the wingcases get very close to each other dorsally around the union of the thoracic with the abdominal segments, which is the narrowest point. Color light green ventrally with fine criss-crossing, vein-like pattern, darker lines on wing cases. Along each antenna there are two lighter warts. Dorsally light green also with a subdorsal dark green longitudinal stripe on either side from cremaster to distal end of wingcases, giving the impression of a partly rolled leaf. Measurer 3.8 cm long, 1 cm laterally at widest point and .8 cm dorso-ventrally at widest point. Lasts 11 days.

Adults. No noticeable sexual dimorphism in this species. Shape of forewing: slightly convex costal margin, rounded apex, almost straight but faintly sinuose outer margin, rounded tornus and straight inner margin. Hindwing with almost straight costal margin, rounded outer angle, continuing in the rounded and faintly sinuose outer margin, rounded anal angle and almost straight and folded inner margin.

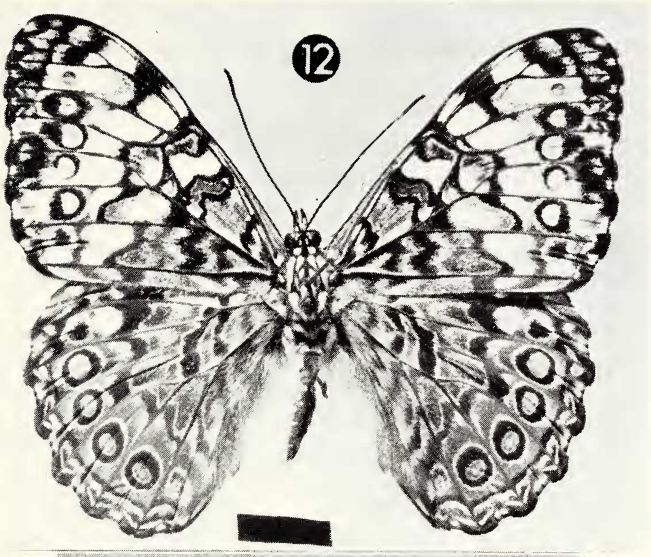
Colors dorsally mostly dark gray with bluish tinge on forewing apex and along hindwing outer margin, with whitish markings, mostly on forewing, forming a complicated pattern of bars, lines and circles. There is a conspicuous S-shaped reddish marking at the mid-

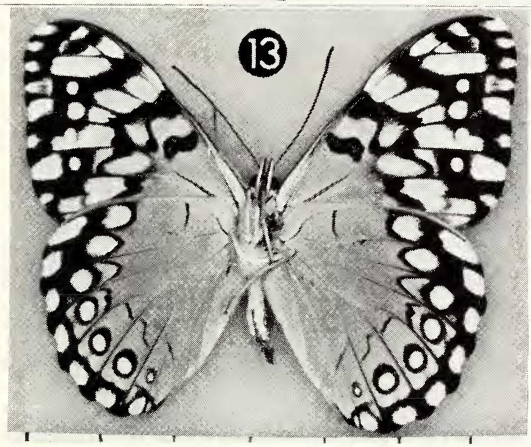
costal margin directed towards the center of the forewing. Ventrally the dominant color is beige, which covers the basal third of forewing and two-thirds of the hind wing. There is a replica of the dorsal pattern of dark brown and yellowish white on the apical zone of both wings. The reddish S marking is also present, even more conspicuous, due to the sharp contrast of the reddish color with the ventral lighter coloration. The body is dark gray dorsally, cream colored ventrally; eyes reddish-brown; proboscis orange; antennae black with white ventral spots on each segment; and a tiny orange spot at the tip. Average wing span 7 cm in males, 7.5 cm in females. Total developmental time varies between 33 and 37 days.

NATURAL HISTORY

The adults of *Hamadryas guatemalena* in El Salvador frequent wooded areas bordered by open, low brushy land, and are usually seen perching on tree trunks with their wings spread open, head pointing down. Several individuals might thus be seen in neighboring trees and from time to time aerial encounters occur, with many "click-clicks" emitted while rapidly chasing each other. This characteristic is limited to the males. The adults do not feed on flowers, but come often to the ground to suck the juices of fermenting fruits. Mangoes, guayavas, jocotes (hog plums) and the fruit of a local rubber-tree (*Castilla gummifera* Pittier) seem to be preferred. They also feed from exudations from various trees. When they feed on the ground, the wings are at times held perpendicular to the back. When they are feeding on the tree-trunks, the wings are always spread open. The females ready to oviposit fly close to the ground, more slowly than usual, until a foodplant is located. They alight usually under a mature leaf and deposit one egg while the wings are apposed dorsally. Several eggs might be deposited on a single vine, always on the underside of a leaf. At times two, and rarely three eggs are deposited one on top of the other, but never have we seen a female deposit two or more eggs side by side on the same leaf. When more than one egg has been found side by side under the same leaf, their hatching is not simultaneous, but separated by a day or two, indicating successive ovipositions by the same or different females.

The hatching larvae eat an exit hole from the wall of the shell and might eat part of a wall. They never consume the whole eggshell. The small larvae move to the edge of the leaf, bare a vein by eating the tissues around it, and prolong the bared vein by affixing to it, with silk, small frass pellets, using this artificial perch as a resting place during first and second instars. Very often the small larvae affix excrement pellets to their own body, probably for protective purposes. It is worthy of mention that when two or three eggs have been deposited one on top of the other the hatching larvae do not damage the ones on top due to their acquired habit of eating the exit hole on the side of the eggshell. Damage to the egg on top would be unavoidable if the larvae should eat the exit hole from the upper part of the eggshell as is usual in most species of butterflies. The larvae are usually solitary, but when two





Figs. 12 and 13. *Hamadryas guatemalena* Bates. 12. Male, dorsal view. Black bar 1 cm. 13. Male, ventral view. Scale in cm.

or three eggs are deposited as described, the ensuing larvae make their resting perches independently, but on the same leaf, and might stay together during the whole larval stage without bellicose interaction. When the third instar is reached, the resting perch is abandoned and the larvae spend most of the day motionless on top of a leaf, with the thoracic segments humped and the head bent so that the horns are parallel to the leaf surface. The larvae of *H. guatemalena* are slow moving and rather passive. The spines which cover most of the body do not have urticant properties. When ready to pupate the larvae

weave a silken mat on the stem of the vine or under a leaf, clean their digestive tract and hang from the chosen spot for a day with their thorax and head incurved ventrally and shed their larval skins. The pupae are firmly anchored to the silk pad, due to the flat surface of the cremaster. If the supporting stem is rolled one way or another the pupae will follow the movement rigidly, "standing" on their cremaster. When disturbed the pupae wiggle laterally and vigorously for a few seconds and stop moving, usually bent to one side. After a time, they revert to the vertical position.

The adults emerge rapidly from the pupashell and hang from it while ejecting a reddish meconium and expanding their wings. When the wings are rigid enough, the butterflies take flight. From then on the wings are usually kept spread while at diurnal perching.

This species is subject to heavy parasitism by tachinid flies, which abandon the host as larvae and pupate on the ground. This happens during the last larval instar or during pupation of the host.

The larval foodplant in El Salvador is *Dalechampia scandens* L., an Euphorbiaceae vine which in our own experience is used by other species of *Hamadryas* (Muyshondt & Muyshondt, 1974) and other species of Nymphalidae, such as *Catonephele nyctimus* Westwood, at least two species of *Dynamine*, and *Mestra amymone* Ménétries. The plant is quite abundant along fences, ravines and in the borders of wooded land, up to about 1500 m altitude, which is also the range where *H. guatemalena* is found. The leaves and bracts of the plant have urticant properties.

It is to be noted that *H. guatemalena*, *H. februa* and *H. amphinome* share not only the foodplant but the habitat as well. It is quite common to see these species, especially *guatemalena* and *februa*, fly in the same neighborhood.

DISCUSSION

Descriptions of the early stages of species belonging to this group of butterflies have been published in the past under the generic name of *Ageronia* (Müller, 1886; Seitz, 1916), but to our knowledge this is the first description illustrated with photographs ever published on the early stages of *Hamadryas guatemalena*.

Butterflies belonging to this group have been called by various authors under different generic names as a whole: *Ageronia* (Müller, 1886; Holland, 1914), *Hamadryas* (Klots, 1960; Ehrlich & Ehrlich, 1961) and have been usually grouped under subfamily Ergolinae (Klots, *op. cit.*), or tribe Ergolini (Ehrlich & Ehrlich, *op. cit.*). The adult shape, coloration and behavior is so peculiar and similar in all of the species that it is only natural to consider the various species as forming a well defined group within the Nymphalidae. Even during the early stages the different species share many characteristics:

the egg shapes of *H. guatemalena* and *H. februa* (Muyshondt & Muyshondt, 1975), and according to Müller (1886) the eggs of other species also, are so similar as to make it hard to tell apart, if at all possible, one egg from another. The same thing is true, to a point, with larvae and pupae; they all use the same group of foodplants (*Dalechampia* spp.), and exploit about the same habitats. Yet there are also marked differences among them, which might prove true some authors' contention (Müller, 1886; Burmeister, as cited by same Müller, *op. cit.*) that there are marked sub-groups within the genus *Hamadryas* Hübner, which might make it convenient to determine the proper placement of the species within the group and the use of the names *Ageronia* Hübner, *Peridromia* Boisduval, *Amphichlora* Felder in addition to *Hamadryas* itself. All these are available generic names according to Hemming (1967).

We will point out the differences we have observed between *H. februa*, *H. guatemalena* and *H. amphinome* and will use the observations made by Müller on some of these and on other species to make the point evident. The eggs of *guatemalena*, *februa*, *sp. ign.* (in Müller), *fornax* and *arete* have the same kind of sculpturing. Not so the eggs of *amphinome*, which are almost smooth. The larvae of *guatemalena*, *fornax*, *epinome* and *amphinome* have dorsal spines only on segments A-7 and A-8, whereas these dorsal spines are present on all abdominal segments in *februa*, *arete* and *sp. ign.* The pupal head prolongations vary also from species to species: they are about the same in *guatemalena* and *arete*, being laterally divergent and incurved dorsally. In *februa* they are partially fused and follow the axis of the body. Then in *epinome*, *sp. ign.*, *fornax* and *amphinome* they are divergent laterally, but follow the axis of the body, as seen laterally.

As for larval behavior, *guatemalena*, *februa*, *epinome*, *sp. ign.* and *arete* have solitary habits and all of them construct the resting perch with frass pellets on the edge of the leaf. This is not the case with *fornax* nor with *amphinome*, which have acquired gregarious behavior during the larval stage and have given up the perch-making practice. *Amphinome* in addition has developed a very angry and excitable disposition. Pupal behavior is the same in all species we have observed, and corresponds with Müller's description except for his reported light sensibility. They all wiggle violently when disturbed and might remain bent to one side for some time afterwards. Contrary to this, the adults we have observed (Müller does not mention adults behavior) of *guatemalena*, *februa*, *amphinome*, *fornax* and *glauconome* Bates, all show the same peculiar jerky flight, the frantic clicking when males encounter each other, or when chasing intruders, the feeding on fermenting fruits and tree wounds plus the characteristic wing-spread attitude while perching on tree-trunks.

According to Müller, Burmeister grouped the species in the following manner: 1) *feronia*, *ferentina* and *fornax*. 2) *amphinome*, *arete*, *arethusa*, related

to *chlöe*. Müller himself did it as follows: 1). a.—*amphinome*, b.—*epinome*, *sp. ign.*, *fornax* (*ferentina*); 2).—*arete*, *arethusa*, proposing to put back in use the genus *Peridromia* for the latter. For him *chlöe* (the type species of *Ageronia*, according to Hemming) would be an intermediate form between *amphinome* (which is the type-species for *Hamadryas*) and *epinome* (which he places with *fornax*). So it looks as though *Hamadryas* should apply to *amphinome* and whichever species are found to be congeneric with it; *Ageronia* to *chlöe* and whichever species are congeneric with it; *Amphichlora* to *feronia* and whichever species are its congeneric and *Peridromia* to *arethusa* and its congenerics. Unfortunately we do not have reference material against which to compare our species, so we are not in a position to establish which is the type-species corresponding to *guatemalena*. We leave that to the taxonomists.

It is worthwhile to point out that there is interbreeding between closely related species in nature: *Limenitis arthemis astyanax* Fabricius × *L. archippus* Cramer (Klots, 1959; Platt & Greenfield, Jr., 1971), *Vanessa atalanta rubria* (Frühstorfer) × *Cynthia annabella* Field (Dimock, 1973), and as a consequence hybrids have been found to result under natural conditions. Hybrids have also been produced in the laboratory from crosses between species naturally separated by great distances, such as *Papilio asterias* × *P. machaon* (Clarke & Knudsen, 1953), *Papilio polyxenes asterias* × *P. maackii* (Clarke & Sheppard, 1964), and several others, what seems to prove close specific relationship between them, even if living far apart from each other under natural conditions. Yet, even if *H. guatemalena*, *H. februa* and *H. amphinome* dwell in the same habitat, during all months of the year, and are in addition grossly similar to each other, we have never found evidence of interbreeding, nor have we seen interspecific copulations, nor have we known of any report thereof. That by itself would seem to indicate these species are not so closely related, as their aspect and other characteristics suggest, as to belong to the same genus. Unfortunately our efforts to have males and females of the different species copulate in captivity have failed (actually, even attempts to obtain copulation with males and females of the same species have proved unsuccessful), so we can not bring forth proofs in either way.

We emphasize that in *H. guatemalena* the color of the larva during the 4th and 5th instars becomes very conspicuous by its contrasting colors, which makes it an easy task to locate the larvae against the green leaves of the foodplant on which they usually rest quite in the open. This daring behavior would seem to advertise impalatable conditions, bad flavor or poisonous properties, to eventual predators. In this respect *H. guatemalena* seemingly has an advantage over *februa*, whose colors are not so gaudy. Probably an increased impalatability compensates for the loss of the additional mechanical protection the dorsal spines (missing in *guatemalena*) provide *februa*. The pupae of

this species, as in many other protected species, are exceedingly cryptic, imitating to perfection a partly rolled leaf, but rely also on the vigorous wiggling, which might scare away predators, as protection. The adults, even though they display an aggressive disposition by rushing at any intruder in their territory, exploit camouflage to perfection, blending their complicated wing color pattern to moss and lichen growing on the tree-trunks on which they rest with the wings spread open.

Euphorbiaceae plants have been historically reputed for their caustic and/or poisonous fluids. *Dalechampia scandens* belongs to this family, and the leaves and bracts have urticant properties. It would seem logical to deduce from this and from the larval coloration and behavior, that *H. guatemalena*, which feed exclusively on that plant, could have developed chemical protection against predators derived from noxious components of the plant. Furthermore we find that the species is heavily parasitized by tachinid flies during its larval stage. We have pointed out in the past (Muyshondt 1973 a, b; Muyshondt & Muyshondt, 1974) the repeated coincidence of heavy parasitism suffered by many species generally accepted as protected by poisonous plant derivates and species suspected as protected. *Hamadryas guatemalena* is another species which might be added to the list.

Literature Cited

Clarke, C. A. and J. P. Knudsen. 1953. A hybrid swallowtail. An account of the "cross" *Papilio asterias* ♀ (North American Black Swallowtail) × *Papilio machaon* ♂ (The Swallowtail, of European-Malta-Stock) and a note on the "*machaon complex*" of the North American Continent. Entom. Record, **65**: 76–80.

——— and P. M. Sheppard. 1964. The hybrid between *Papilio polyxenes asterias* Fabr. female and *Papilio maackii* Men. male (Lepidoptera, Nymphalidae) [*sic*]. Entomologist, 131–133.

Dimock, T. E. 1973. Three natural hybrids of *Vanessa atalanta rubria* × *Cynthia annabella* (Nymphalidae). Jour. Lep. Soc. **27**: 274–278.

Ehrlich, P. R. and A. H. Ehrlich. 1961. How to know the butterflies. Wm. C. Brown Co. Publishers. Dubuque, Iowa.

Hemming, F. 1967. Generic names of the butterflies and their type-species. Bull. Br. Mus. Nat. Hist. (Ent.) Suppl. 9.

Holland, W. J. 1914. Butterflies. Doubleday, Page & Co. New York, N. Y.

Klots, Alexander B. 1959. A mixed mating of two species of *Limenitis* Fabricius (Lepidoptera, Nymphalidae). Jour. New York Ent. Soc. **67**: 20.

———. 1960. A field guide to the butterflies. Riverside Press. Cambridge.

Müller, W. 1886. Südamerikanische Nymphaliden Raupen. Versuch eines natürlichen Systems der Nymphaliden. Zoologische Jahrbuch. 453–461.

Muyshondt, A. 1973*a*. Notes on the life cycle and natural history of butterflies of El Salvador. III A.—*Temenis laothöe liberia* Fabricius (Nymphalidae-Catonephelinae). Jour. N. Y. Ent. Soc. **81**: 224–233.

———. 1973*b*. Notes on the life cycle and natural history of butterflies of El Salvador. IV A.—*Pseudonica flavilla canthara* (Nymphalidae-Catonephelinae). Jour. N. Y. Ent. Soc. **81**: 234–242.

——— AND A. MUYSHONDT, JR. 1975. Notes on the life cycle and natural history of butterflies of El Salvador. I B.—*Hamadryas februa* (Nymphalidae-Hamadryadinae). Jour. N. Y. Ent. Soc. **83**: 157–169.

PLATT, A. P. AND J. G. GREENFIELD, JR. 1971. Interspecific hybridization between *Limenitis arthemis astyanax* and *L. archippus* (Nymphalidae) Jour. Lep. Soc. **25**: 278–284.

SEITZ, A. 1915. Macrolepidoptera of the World. Vol. 5. Stuttgart.